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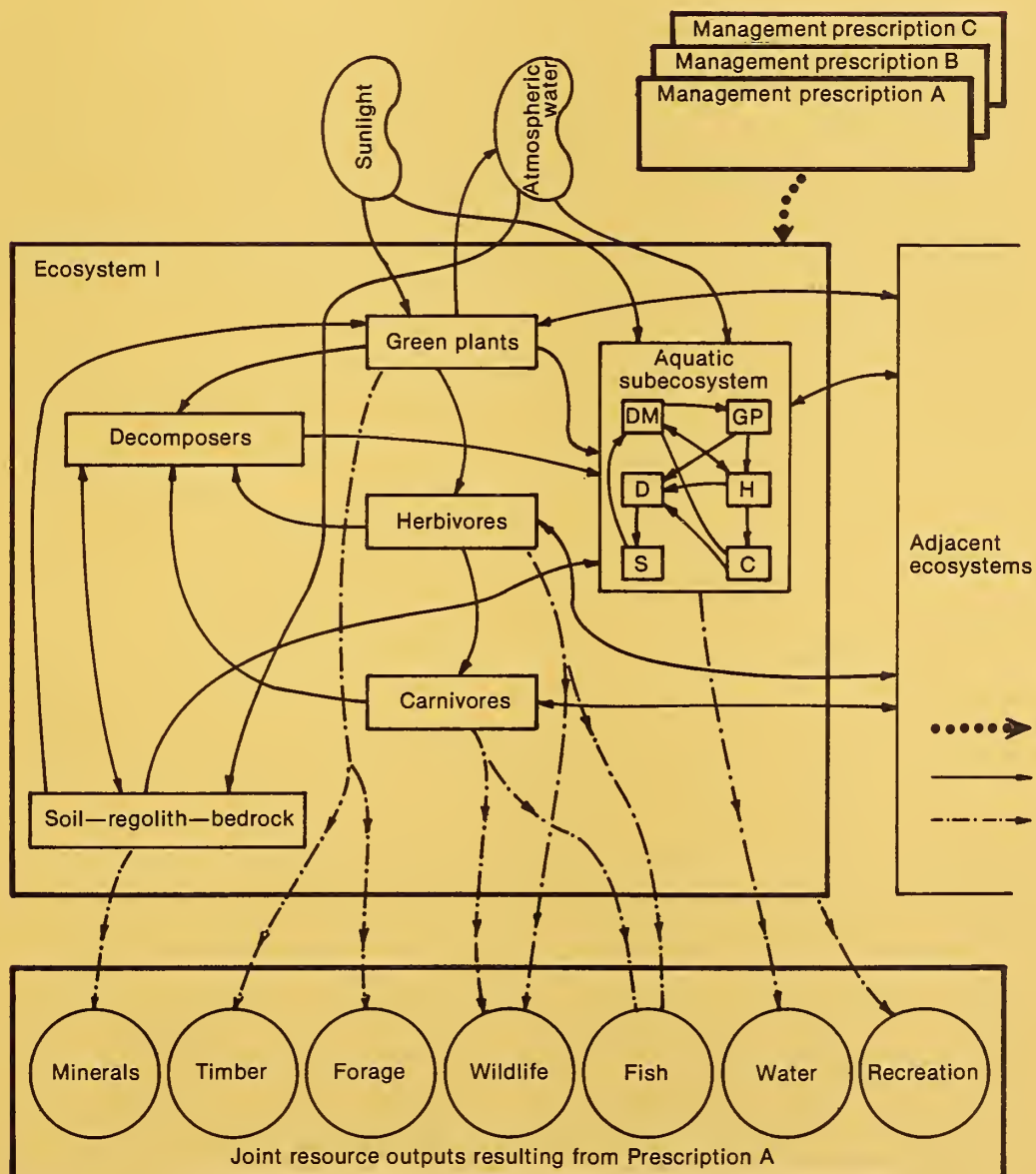
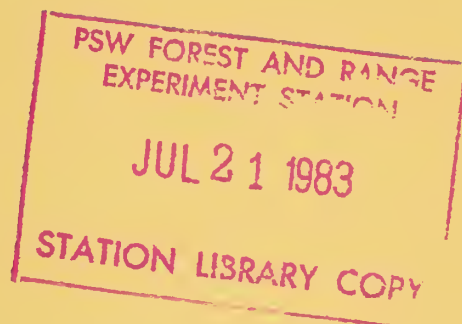
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Analysis of Forage Production for Assessments and Appraisals

John E. Mitchell



Abstract

This report is an overview of the biotic and abiotic ecological factors, including human activities, that affect forage production on forest and rangeland ecosystems. Also discussed are forage production models and how forage quantity and quality can control animal production.

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Analysis of Forage Production for Assessments and Appraisals

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Management Implications

An understanding of the ecological factors affecting forage production is necessary if natural resource scientists are to develop models and other analytical tools that will more accurately and precisely estimate the forage response to management practices on specific ecosystems.

Although the present knowledge on this subject is fairly comprehensive in several general areas, it is incomplete in others. Environmental factors related to processes that can be measured aboveground have been described to a much greater degree than those interacting with plants belowground. For example, scientists have described the ecological consequences of light intensity and CO₂ concentration on photosynthesis more exactly than they have described belowground nutrient cycling pathways. Fortunately, increasing research in edaphology, nutrient cycling, and some aspects of ecophysiology is adding to knowledge of belowground ecological processes. Most techniques for estimating forage production on the ground have been known for some time; however, procedures for predicting forage production on the basis of climate, management, and other causal factors are more recently and less finely developed.

Researchers have been able, however, to construct reasonably accurate models of the rate some species and species groups accumulate biomass. To date, such models have tended to be applicable only to specific plant communities, which narrows their usefulness in predicting responses to management at the regional or forest level. Models are being improved so that, within the coming decade, the use of ecological production models is likely to play an important part in resource management procedures. The most apparent obstacle in this modeling is a lack of an accepted general systems theory paradigm applicable to natural ecosystems. A general systems approach is based on the idea that system properties are not a function of characteristics of each ecosystem, but can be applied universally to many ecosystems (Halfon 1979).

This report presents an overview of forage production as an ecological process. It describes production mechanisms for ecological modeling in a way that can be readily synthesized. In addition, it provides the reader who is familiar with basic concepts of ecology with a contemporary picture of what forage production is and, using current analysis tools, how it may be evaluated within the framework of natural resource assessments.

Introduction

Concept of Production

The concept of productivity, developed from the theory of ecosystem trophic structure (Lindeman 1942), is fairly new to ecology. Productivity is closely related to the ecosystem process of energy flow, which begins with short-wave solar energy and ends in the form of organismic heat of respiration (Odum 1971). In general, productivity refers to the rate at which energy is bound by organisms in the form of biomass. The units of productivity are most commonly expressed in terms of biomass per unit area per unit time (e.g., g·m⁻²·week⁻¹, kg·ha⁻¹·year⁻¹), although it is sometimes given in terms of energy (e.g., kCal·m⁻²·year⁻¹) (Whittaker 1975). Conversions between energy and biomass have been made (Golley 1961), but the relationships appear to be somewhat dynamic, both among species and temporally within species (Slobodkin 1962, Darling 1976).

Several other terms closely tied to productivity have created confusion in the ecological literature. These terms include words such as production, yield, biomass, phytomass, and standing crop. The relationship between the terms "productivity" and "production" is an excellent example. Although there is little disagreement on

the meaning of productivity as a rate process, the same is not the case for the meaning of production. Texts in pure and applied ecology contain many different definitions, stated or implied, of production. According to the predominant opinion, production is defined as the biomass or energy incorporated into an ecosystem during a specified time period (often a season or a year). As such, both productivity and production are rate processes and may be used interchangeably (Odum 1971). Authors using the term production to describe an amount of accumulated biomass (Smith 1974) have nearly always presumed a time factor as part of their definition. In this report, therefore, the terms productivity and production are used synonymously (Rodin and Bazilevich 1967, ESA-AAAS 1968). Odum (1971) properly suggested that the time interval should always be explicitly stated when the term production is used.

Biomass, unlike production, refers to an amount of live material present at any given time on a per-unit-area basis. It, too, may be expressed in terms of either mass (e.g., g·m⁻², kg·ha⁻¹, lb·acre⁻¹) or energy (e.g., cal·m⁻²). A good illustration of the difference between production and biomass is provided by a bucket with a hole in its bottom, hanging under a running faucet. The rate at which water runs into the bucket would be equivalent to production, and the amount of water in the

bucket at any one time would represent biomass. Mathematically, the relationship between production and biomass is as follows:

If X = biomass

$$\frac{\Delta X}{\Delta t} = \text{change in biomass with respect to time } t$$

$$\frac{\Delta X}{\Delta t} = \text{production} - \text{death}$$

(assuming no emigration or immigration)

To determine biomass from production, one would have to estimate the death function and integrate the equation between times t_1 and t_2 .

Phytomass is a recently coined term referring to plant material only; it is the total mass of plants, including dead attached parts, per unit area at a given time. It differs from biomass because it includes dead attached organic material. Standing crop is generally considered to be synonymous with biomass (Petrusewicz 1967); however, some authors have denoted it as being equivalent to phytomass (Barbour et al. 1980). The meaning of standing crop should be defined when the term is used.

"Yield" has had more of a colloquial use, primarily in applied facets of ecology. According to a preliminary Range Inventory Standardization Committee (RISC) report (Artz et al. 1980), yield is "(1) the quantity of a product in a given space and/or time; (2) the harvested portion of a product." Because of its uncertain and multiple meanings, yield is not commonly used in the ecological literature.

Primary Versus Secondary Production

Primary production refers to the rate of fixation of solar radiation by autotrophic organisms (green plants) through the process of photosynthesis. The total rate at which energy becomes fixed is called gross primary productivity (GPP). Not all of this energy is transformed into biomass, however. In most ecosystems, more than half the energy in GPP is used immediately in respiration to supply the necessary energy for the plant's own metabolism (Woodwell 1970). The remaining fixed energy, stored in plant tissues as biomass, is called net primary productivity (NPP).

Secondary production is the rate at which energy, in the form of organic tissue, is converted into animal biomass by digestion of consumed material. The energetics of secondary production are somewhat more complex than those for primary production. Figure 1 is a schematic representation of the relationship between consumption and secondary production. In brief, secondary production equals assimilation less respiration, while the energy of assimilation equals consumption less food unused (i.e., feces and urine). In addition, not all food removed by the consumer is, in fact, ingested (Mitchell and Pfadt 1974).

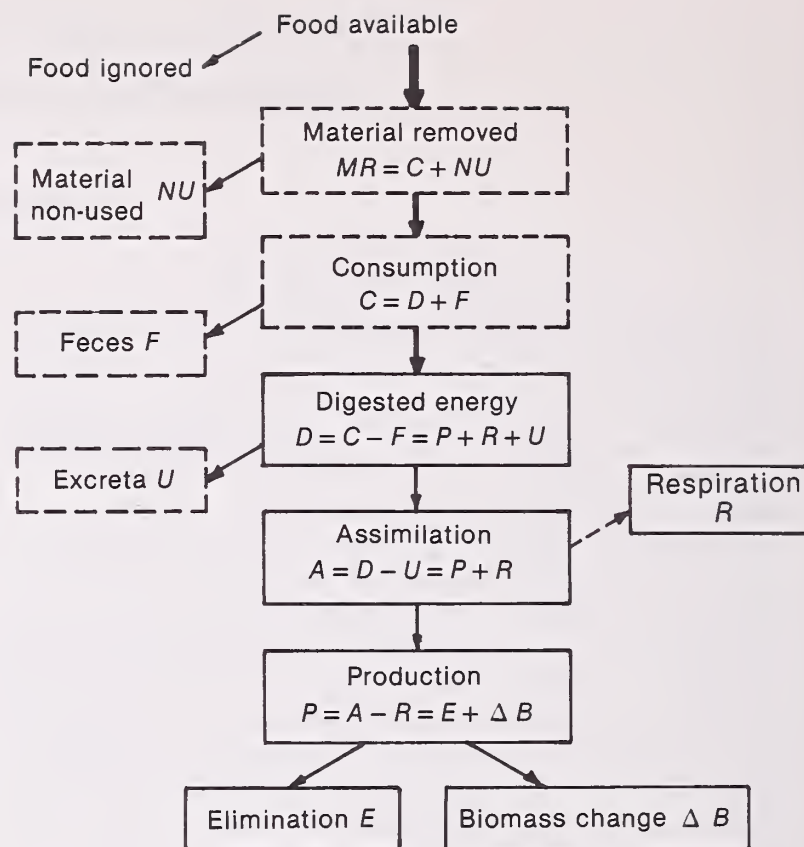


Figure 1.—Schema of energy partitioning between food available and secondary production. Note that biomass dynamics is a function of both production and losses of biomass (E) caused by death and emigration, a relationship that exists at each trophic level. (Adapted from Petrusewicz 1967.)

Secondary production includes the process of animals eating plants (herbivory) and animals eating other animals (carnivory). Herbivores are called either primary consumers or secondary producers in ecosystem-level ecology. Carnivores are also termed secondary consumers.

Actually, from an ecosystem viewpoint, an additional kind of food chain exists besides the herbivore/carnivore chain; it is the detritivore chain or food chain of decay (Odum 1971). This chain cannot be considered in terms of secondary productivity, as such energy is not stored as biomass but, rather, in the form of dead organic matter and decay organism populations. In this review, the detritivore food chain is treated as only a mechanism for converting dead organisms to heat, thereby balancing the ecosystem energetics equation. Phillipson (1966) provides a readable, basic overview of ecological energetics.

In comparison to available energy, neither primary nor secondary production is very efficient thermodynamically. According to Woodwell (1970), considerably less than 1% of the incoming solar energy is used in photosynthesis. This tiny fraction is sufficient, nonetheless, to support the entire biosphere. At the secondary levels of production, the amount of energy transferred varies widely in terrestrial ecosystems. Lindeman's so-called "10 percent law," which states that about 10% to 20% of the energy entering a trophic level can be utilized without perturbing the ecosystem, is probably a reasonable assumption in general terms, at least for natural communities. This ratio of energy

actually fixed through production by a population or trophic level to energy available is called ecological efficiency (E) (Hanson 1962).

The number of trophic levels in an ecosystem is limited by its ecological efficiency. If E is constant, then the energy available at any trophic level would be E^i , where i is the mean number of food-chain links between that trophic level and the autotrophs (Slobodkin 1962). For example, if $E=0.15$ and the system consisted of a grass-mouse-coyote food chain, the coyote would have only about 2% of the energy in the grass incorporated into its production ($0.15^2=0.0225$). This is one reason why terrestrial systems seldom have more than three or four trophic levels.

Comparison of Ecosystem Components and Resource Products

A conceptual difference exists between ecosystem production, and resource products. For example, the process of energy flow addresses the movement of carbon (energy) into, through, and out of an ecosystem. If the carbon entering and leaving primary producer components are integrated over a given time period, the quantity obtained can be converted to biomass outputs which characterize those ecosystem components.

In contrast, resource products refer to specific outputs from ecosystems which provide some use to mankind. Generally, they comprise a subset of outputs from comparable ecosystem components. For example, forage as a resource product only consists of the portion of accumulated plant biomass which is suitable and available for consumption by specific categories of herbivores (Fig. 2). Although relationships exist between primary production and available forage on rangeland ecosystems, objective translation mechanisms generally are not available.

The ecosystem concept began to be used as a basis for natural resource management in the early 1970's. Before then, management connoted manipulation of only the "resource," without regard to the interactions or whole-system responses involved. With the increased sophistication of systems analysis, the enhanced understanding of ecosystem processes and interactions, and recognition of the lack of effective translations between systems ecology and single-resource management concepts, it was clear that an ecosystem-level approach to the subject was necessary. More recently, management has come to denote the simultaneous manipulation of the entire ecosystem, even though some components are obviously affected more than others (fig. 2). For the most part, this paper addresses those ecosystem processes which are related to primary and, to some extent, secondary production.

Techniques for Estimating Production

Direct Estimates

Historically, the concept of primary productivity came before, and served to further, the interest in

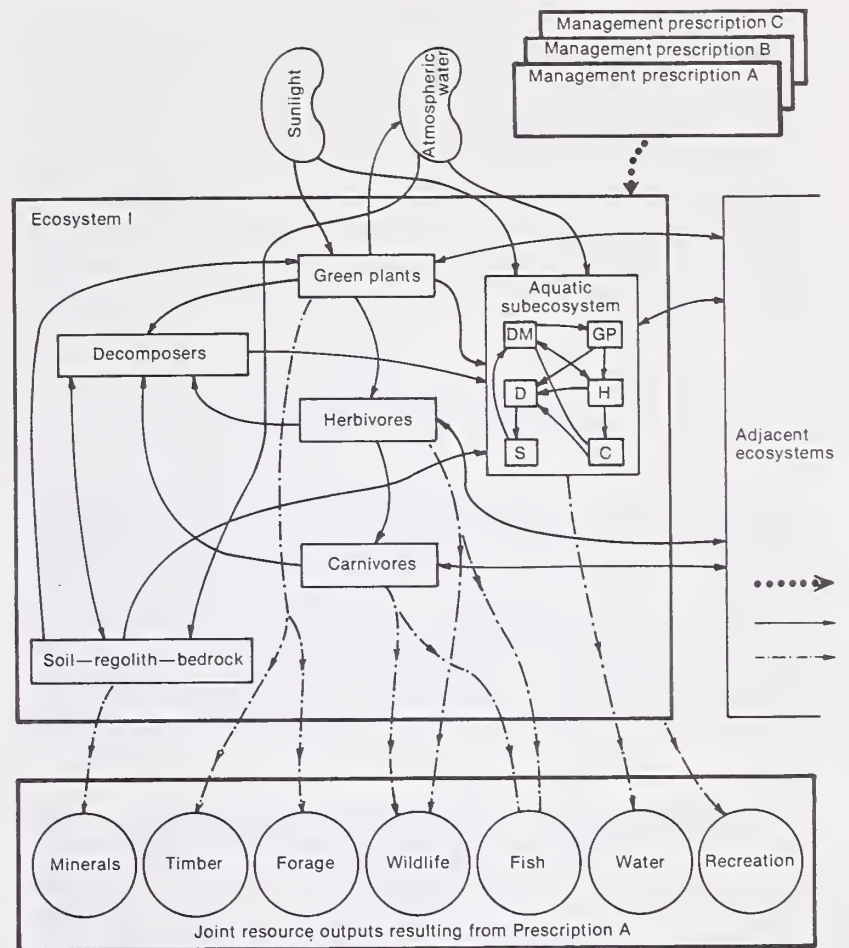


Figure 2.—Ecosystem structure and resource outputs. Management prescriptions are applied to ecosystems, producing an array of resource outputs. Nonresource energy and nutrient losses from ecosystem are implied but not shown.

secondary productivity (Odum 1968). Following this logical flow, primary production and the ways it can be estimated are examined first. Before discussing production, however, it is helpful to outline the difference between direct and indirect production estimators.

Primary productivity is the rate of photosynthesis of all plants in the ecosystem being described, and is expressed in terms of energy transformed. A direct estimate of primary production, then, involves the actual measurement of photosynthesis. Such instantaneous measurements of rate processes $\Delta X/\Delta t$ can be either reported where $\Delta t \rightarrow 0$ or averaged over longer time intervals.

Methods for directly estimating photosynthetic rates are associated with monitoring the change of carbon dioxide or oxygen concentrations during photosynthesis. Carbon dioxide flux is more suited than oxygen flux for estimating photosynthesis, because slight variations in the amount of CO_2 taken up are easier to detect (Sestak et al. 1971). This is because of the small concentration (300 p/m) of CO_2 in the atmosphere in comparison to O_2 .

Woodwell (1970) attempted to estimate GPP of an entire community by monitoring the flux of CO_2 in the canopy, at night, during temperature inversions in order to obtain an estimate of community respiration. His measurements may have been accurate but such estimates can only be considered approximations. Most work on GPP using CO_2 exchange has involved the

monitoring of plants or parts of plants. A comprehensive review of gas exchange, especially as it applies to forage plants, is provided by Moore (1977).

Estimating production indirectly involves relating it, as a dependent variable, to some other measured attribute. For the most part, ecologists have used indirect methods to determine NPP, and their prevalent algorithms have utilized biomass as the directly measured, independent variable.

Biomass as an Estimator of Production

Most forage plants, especially herbaceous species, go through contrasting phenological stages between germination and maturity. Consequently, the respiratory demands of growing or storage tissue and the photosynthetic supply from leaf tissue of varying age and photosynthetic capacity are constantly changing (Moir 1969). This can result in dynamic relationships between NPP and biomass, especially at the community level.

In a monoculture system, a single measure of biomass is adequate to accurately predict production. This is especially true when the species present possesses a C-3, cool-season photosynthetic pathway (C-3 plants, biomass accumulate continuously until soil-water stress or some other factor induces dormancy, with little growth thereafter; in comparison, C-4 plants often have multiple growth periods reflecting precipitation patterns). In such a case, peak standing crop and NPP are nearly equivalent (Wiegert and Evans 1964).

In ecosystems of greater diversity, the standing crop or biomass at any given time is often much less than the NPP (Malone 1968). Each species of such a community may be unique phenologically and, therefore, possess unique rates of development and times of peak standing crop (Singh et al. 1975). Forbs are particularly conducive to shattering after senescence, resulting in their complete absence shortly after maturity. Moreover, according to Moir (1969), species in natural ecosystems, through natural selection, do not generally accumulate the products of NPP in large storage organs or easily harvested parts. This is in contrast to monoculture species, which often have such attributes as a result of selective breeding by man. Therefore, it is likely that community peak standing crop will serve as an adequate indirect estimator of NPP in a simple ecosystem, but not in a diverse ecosystem.

Forested ecosystems do not have NPP levels that approach their standing crop, except during earliest seral stages of succession. Nonetheless, if production and standing crop of only the usable forage in a forest (i.e., herbaceous species and twigs and leaves of browse species) are considered, the concept of community standing crop can serve as a reliable measure of NPP in structurally simple ecosystems. In such cases, the "ecosystem" would be defined only by a forage component.

Odum (1960) discussed the shortcoming of using community peak standing crop to determine NPP and dem-

onstrated that this problem could be minimized by summing the peak standing crop of each species independently. Such a technique, however, may overestimate productivity if a community is dominated by many species with low standing crops (Wiegert and McGinnis 1975). The overestimation results from the inherently high variation in biomass of such species (i.e., because peak standing crop often maintains itself long enough for more than one sample to be taken, use of the highest value obtained overestimates the mean peak standing crop).

The determination of biomass in natural systems is not usually an easy task. If the objective is to estimate NPP on an annual basis, only the current year's growth should be measured, not all living tissue. Graminoids are the easiest group from which to derive biomass data; like all herbaceous species, they die back to the ground each year, and their aboveground parts tend to stay attached to the plant beyond peak standing crop. Forbs, although herbaceous, sometimes have phenological developments in which earlier-developing parts dry and drop from the plant before senescence.

In addition to problems of determining biomass, significant errors in estimating NPP can accrue when vegetation losses are not adequately considered (Wiegert and Evans 1964). Bradbury and Hofstra (1976) found, for example, that including vegetation death in their production estimates in a grassland community increased the estimates by up to 200%.

Woody plants pose a much larger obstacle to estimating biomass than do herbaceous species. To account for biomass accumulated in a given growing season, at least five components must be examined (Whittaker 1962): leaves, twigs, branch growth, stem growth, and root growth. The effort is even more arduous for evergreen species; they require separation of current year's leaves from older leaves and, on some species, the assessment of increase in old-leaf weight (Whittaker 1962). Published work pertaining to woody-plant production is scarce. Most work on trees has, expectedly, focused on the bole, while the preponderance of research dealing with shrubs has dealt with only twigs and leaves or "browse." For examples of total production estimates of trees, see Whittaker et al. (1974) and Grier and Logan (1977). In addition to Whittaker (1962), others who have studied total production of shrubs include Burk and Dick-Peddie (1973) and Caldwell et al. (1977).

Because forage production encompasses only part of woody-plant NPP, this report is limited to assessing twig and leaf production of those species which make up the diet of browsing animals. Even when biomass of browse is limited to twigs and leaves, additional measurement problems exist that are not found with herbaceous species (Pieper 1978). For example, when stimulated by browsing or other factors, shrubs tend to develop twigs emitting from lateral buds, resulting in forage growth scattered throughout the canopy space. Variation in growth flushes in spring and late fall often causes difficulty in distinguishing current year's growth from previous growth. In addition, the nature of evergreen

shrubs sometimes causes a problem in determining new leaf growth. Most researchers have used litter traps to ascertain turnover rates of evergreen leaves as a measure of leaf NPP (Burk and Dick-Peddie 1973).

Given the difficulty of assessing shrub biomass directly by harvest methods, some authors have proposed using various crown measurements to predict biomass nondestructively, a procedure termed "dimension analysis" (Whittaker 1975). Such relationships have been developed for several desert shrub species (Ludwig et al. 1975), chaparral vegetation (Bentley et al. 1970), serviceberry (Lyon 1968), and mountainmahogany (Medin 1960).

In a different approach to predicting shrub production, Irwin and Peek (1979) were able to quantify twig biomass of browse species in the cedar zone of northern Idaho in relation to various silvicultural practices. An objective of their work was to incorporate shrub production into Stage's (1973) Stand Prognosis Model. Their projects were based on regression models, developed from 105 stands, using site factors, habitat type, and time as independent variables.

Nondestructive sampling techniques for estimating biomass of herbaceous species have seen common use, also. Among these methods are ocular estimation (Pechanec and Pickford 1937), the use of capacitance meters (Neal and Neal 1973), beta-particle attenuation techniques (Mitchell 1972), and remote sensing spectral analysis (Pearson and Miller 1973, Tucker 1980). Milner and Hughes (1968) and Mannelje (1978) provide excellent descriptive reviews of both destructive harvesting and nondestructive techniques for sampling herbaceous biomass. Several workers have shown that double sampling provides a more precise estimate of plant biomass than using a harvest method alone (Tadmore et al. 1975); in general, the weight (ocular) estimate technique is used as the fast method and clipping, as the slow method (Francis et al. 1979).

Problem of Fluctuations in Production

Information about NPP during a growing or grazing season is extremely useful to range managers, if long-term records on vegetation response to grazing are lacking (Stoddart et al. 1975). However, there are large variations in the amount of forage produced from year to year. The magnitude of yearly fluctuations appears to be greatest in xeric ecosystems. It was documented four decades ago (Lantow and Flory 1940) and dramatically portrayed more recently by Sharp and Sanders (1978) in a photographic series taken in a long-term study within the salt-desert shrub zone. Stoddart et al. (1975) presented a general discussion of NPP fluctuations.

Fluctuations in production of vegetation are accompanied by shifts in species composition (Miles 1979); however, the extent to which these fluctuations are caused by dynamics in species composition has received little interpretive analysis.

Plant NPP fluctuates both between and within growing seasons (Uresk et al. 1975). The rate of biomass ac-

cumulation by most forage plants is an irregular, interrupted process, reflecting the short-term dynamics of NPP (Sims and Singh 1978). As a consequence, the use of peak standing crop as a measure of NPP for a given species may result in significantly underestimating production, especially in regard to those species with continuous or multiple growing periods interspersed with periods of relative dormancy (Singh et al. 1975). In such cases, a better estimate of NPP would probably be provided by summing positive growth increments during each growing period (Kelly et al. 1974).

Finally, the relationships between fluctuation in NPP and responses in secondary production by herbivores have received little attention. Some work on such ecosystem interactions has been handled through the use of simulation models. Examples of a modeling approach to primary/secondary production interrelationships include grassland and grasshoppers (Rodell 1977), pasture and livestock (Smith et al. 1977), and general consumer/producer relationships in grasslands (French 1979).

Estimating Production of Different Levels of Integration

The concept of levels of integration in ecology is important and broadly accepted (Billings 1978). Essentially, this concept states that, in ecology, the individual organism and its environment, the population and its environment, and the biological community and its environment (ecosystem) form separate, but interacting, hierarchical systems.

The levels-of-integration concept has also been applied, by definition, to various levels of ecosystems (Major 1969). Generally, the definition of ecosystems used by ecologists has reflected the structure and function suited to the topic being addressed. Ecosystems have been defined on the basis of a microcosm encompassing much less than a community (Witcamp and Frank 1970); a single plant community (Golley 1965); a small watershed comprising, perhaps, several plant communities (Mitchell et al. 1975); a group of natural communities dominated by the same species (Grier and Logan 1977); monocultures of human origin superimposed over one to several climax communities (Rauzi 1975); a large region comprising many communities (Sala et al. 1981); and the entire North American grassland (Lauenroth 1979). At the largest scale, some workers have described ecosystems in terms of the entire earth or biosphere (Lieth and Whittaker 1975).

A common thread runs through each of these ecosystems, no matter what its level of integration. That is, each ecosystem must exist in both space and time (Kormondy 1976). The spatial distribution of ecosystems is authentic, according to Kormondy (1976), but their exact outlines are somewhat arbitrary because ecosystems are simultaneously interconnected with other ecosystems, both laterally and vertically, as components of larger systems. In other words, ecosystems are open systems to a greater extent than merely allowing for

solar energy and precipitation inputs and respiratory outputs.

Ecosystems, therefore, can be defined and described from small, localized to large, regional areas. Nonetheless, when addressing primary production (or forage production) as a process, models of such systems have appeared remarkably similar; for example, compare Kelly et al. (1969), Bledsoe (1976a), Sauer (1978), Cale (1979), and Fick (1980). In general, NPP or energy flow rates are controlled mechanistically by abiotic parameters such as heat, water, and soil nutrients, and by biotic factors—primary consumers and decomposers (Innis 1975).

Regardless of its level of integration, ecosystem boundaries have been fixed along natural junctures, based mostly on classifications of vegetation or landform. The incorporation of artificial boundaries based on municipalities or land management agencies poses, to systems ecology, a new problem which has yet to be addressed in the literature. It is apparent, however, that ecological analyses of forage NPP, if handled under existing systems theory, will require ecosystems, as opposed to political and management systems, as a basis for model development.

Some land-management planning models are defined along synthetic boundaries (Ashton et al. 1980). Most of these models utilize mathematical programming algorithms, because optimal solutions are desirable and, hopefully, possible for management systems (Jameson 1970). Forage NPP in these models is generally treated as joint production input functions in terms of animal unit months. Such inputs are not a result of ecological simulation modeling, but, rather, a Delphi process (Linstone and Turoff 1975), involving subjective decisions from groups comprised of scientists, land managers, or both. The justification for a Delphi approach has been based on the premise that providing production outputs from natural systems as a result of management practices does not lend itself to precise analytical techniques but can benefit from subjective judgments on a collective basis. Cooper and Zedler (1980) have proposed using interdisciplinary (ID) teams to describe the responses of ecosystems to developmental or management inputs.

At the National Forest level, land-management planning modeling is based around the linear programming models FORPLAN (Johnson et al. 1980) and (to a much lesser extent on rangelands) Range RAM (Jansen 1976). In both of these cases, however, forage production is not modeled. These are assumed to be known in advance, and are usually obtained through the use of ID teams. With the FORPLAN model, for example, data on forage production as a function of various management prescriptions must be provided, in the form of yield tables, as input into the linear programming matrix.

C. S. Holling and his colleagues (Holling 1978) originated a conceptual framework, "adaptive environmental assessment," as a new process for environmental assessment. Their procedure relies on the formation of a core group comprised of people with analytical skills (e.g., computer programmers and statisticians) and

subject-matter skills (e.g., range scientists, economists). The principal difference between a Delphi procedure and that of Holling is in its method of operation. The adaptive environmental assessment procedure uses an interactive process of core-group meetings to develop models, followed by workshops involving decision-makers and managers who use the models to test and evaluate alternative policies. The core group then meets to evaluate and simplify its models, after which another workshop is scheduled, and so on. A Delphi process is not based on such an interactive technique. Although Holling's method was designed to resolve environmental assessment problems, its concept should be useful in developing techniques for determining joint production inputs of optimization models.

A logical extension of the use of optimization models in natural resource decisionmaking would be to couple production-oriented simulation models of natural systems to the mathematical programming models that allocate land and resources. To date, however, there is little literature on this subject. One simulation model, RANGES, has been written to simulate a grassland ecosystem as a link to range economic models (Gilbert 1975). RANGES is a low resolution model (Van Dyne 1978a), meaning that, in this case, it has few state variables (i.e., component parts defining the ecosystem). (See Patten 1971 for a review of terminology used in systems ecology.) A model with high resolution can be generally categorized as having a relatively large number of state variables, being mechanistic rather than empirical in terms of rate process functions and including many of the real system attributes it is attempting to mimic (Van Dyne and Abramsky 1975). The use of ecosystem NPP models in this manner has been extremely limited; the only example of such work is by Hunter et al. (1976).

Theoretically, it should be feasible to couple ecosystem models with economic or social models. Such mechanistic models would provide a sound conceptual framework on which to base the cause-and-effect relationships found in joint production problems and would allow management impacts to be examined quantitatively (Van Dyne 1978b). No research has yet been published that specifically addresses the problem of merging natural ecosystem boundaries and models with the artificial boundaries of management and economic systems. Present knowledge suggests that the production outputs could be handled within the ecosystem model by treating each natural community as a separate subsystem, provided that the proportion of the natural communities were known for the management system.

Abiotic Factors in Forage Production

As previously mentioned, NPP is the net result of photosynthesis less respiration. Therefore, this discussion addresses abiotic factors as they relate to these two physiological processes. Photosynthesis is primarily dependent upon light, temperature, CO₂ concentration, and water (Daubenmire 1974); however, these factors strongly interact in regulating photosynthesis, requiring

a holistic consideration of their effects (Troughton 1975). The identification, in the past 10 years, of two major photosynthetic pathways (Black 1971) has sharpened our understanding of these interactions. Björkman and Berry (1973) wrote an excellent general review of photosynthesis of C-3 (cool season) and C-4 (warm season) forage plants in relation to light intensity, temperature, CO₂ concentration, and stomatal resistance (a measure of water stress). Figure 3 depicts examples of these generalized relationships: (a) C-4 plants possess a relatively high light saturation point in comparison to C-3 plants; (b) the minimum, optimum, and maximum

cardinal temperatures are significantly higher in C-4 plants; (c) photosynthesis in C-4 plants is greater at leaf CO₂ concentrations below 300 p/m (the minimum CO₂ level where photosynthesis can take place is an order of magnitude lower in C-4 plants—5 versus 50 p/m); finally, (d) because C-4 plants are able to operate more efficiently at low CO₂ concentrations, they can keep their stomata closed to a greater degree (lower stomatal conductance) and, therefore, lose less water through transpiration at a given rate of photosynthesis (i.e., C-4 plants have a much higher photosynthetic water-use efficiency under a water-stressed environment).

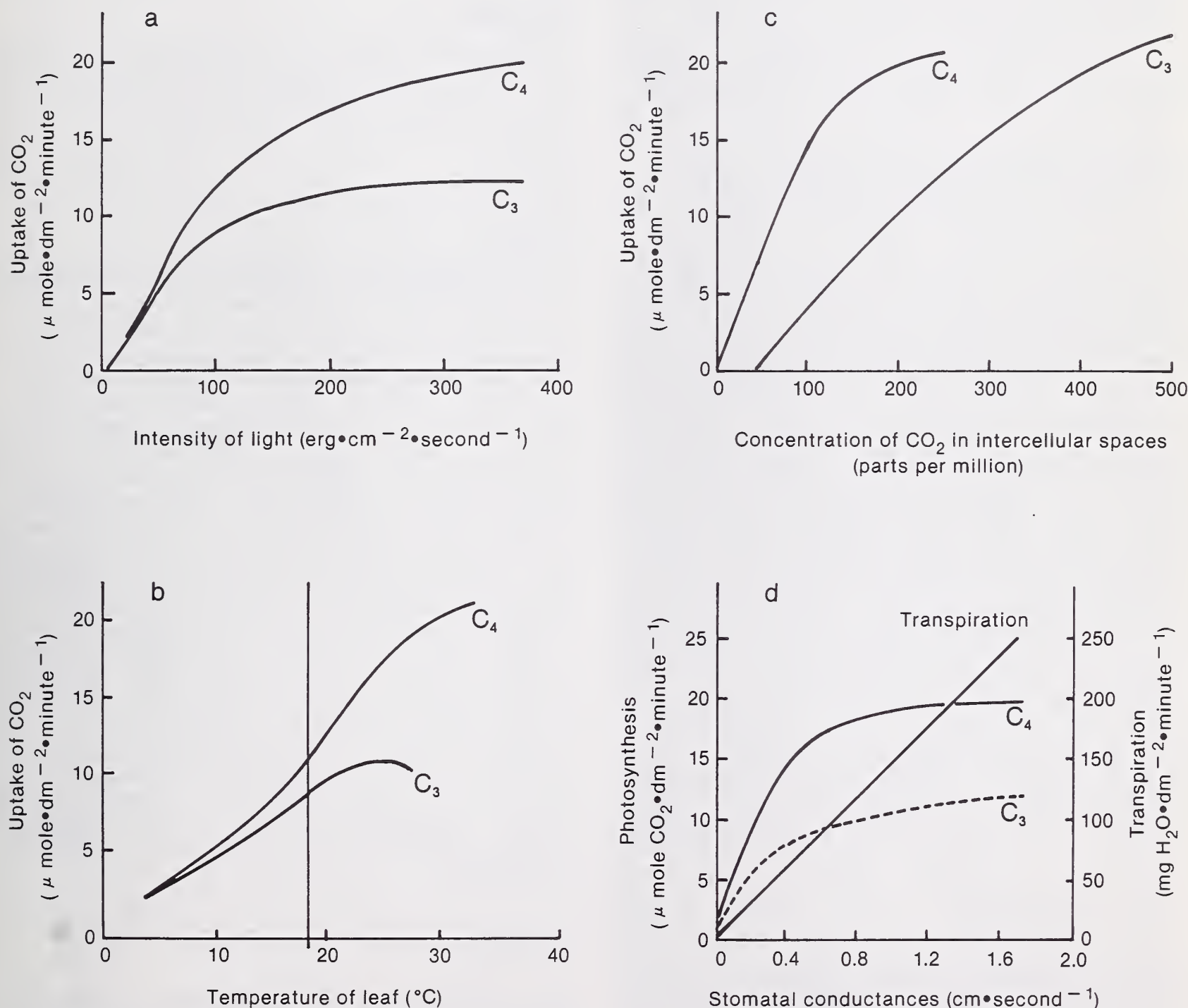


Figure 3.—Photosynthesis of *Atriplex patula* (C-3 plant) and *A. rosea* (C-4 plant) in relation to: (A) light intensity, (B) temperature, (C) CO₂ concentration, and (D) stomatal conductance. (Adapted from Björkman and Berry 1973.)

Climatic Factors

Carbon dioxide concentrations at the leaf surface vary in proportion to wind speed and rate of photosynthesis (Chang 1968); however, the relative importance of CO₂ dynamics in altering NPP for natural forage-producing systems is probably not significant in temperate regions. On grasslands, the canopy is generally insufficient to have a strong attenuating effect on prevailing winds, and in browse-dominated communities, light and temperature are more likely to be limiting factors. As a result, most models simulating NPP primarily utilize light, temperature, and soil water (or precipitation) as exogenous driving variables (Cale 1979; Detling et al. 1979), or just the latter two (Parton 1978), or sometimes only water (Schumacher 1973).

Rice and Parenti (1978) concluded from a field experiment in the tallgrass prairie that higher soil temperature is the main cause of increased NPP after burning or forage removal. They ascribed this relationship to the relatively high optimum temperatures (about 35° C) for growth of the C-4 grasses dominating their study site.

Although primary productivity depends on photosynthesis, NPP is not necessarily closely correlated to the rate of photosynthesis. Respiration, translocation to belowground parts, and other processes constraining a plant's ability to make use of photosynthate, often can have an overriding effect on the accumulation of aboveground biomass (Evans 1975). In fact, the allocation patterns of photosynthate (carbon) by plants into their photosynthetic system (leaves) versus nonphotosynthetic system (support structure, roots) have been postulated to affect NPP as much as or more than carbon gain capacity (Detling et al. 1979). Carbon-gain capacity is defined as the proportion of dry weight of photosynthetic tissue produced in a given time. Mooney (1972) and Thornley (1976) made extensive examinations of carbon allocation in plants and its implications to NPP.

Reductions in NPP caused by increased respiration can be significant, especially in ecosystems characterized by large biomass levels and high temperature (Evans 1975). Early simulation models of community NPP relied upon the assumption that respiration is directly related to leaf area index (LAI) or biomass; however, more recent work has shown that respiration increases geometrically with LAI and is more a function of photosynthesis than of biomass (McCree and Troughton 1966). Further, McCree (1970) proposed, with some basis for acceptance (Penning de Vries 1972), that respiration by plants can be divided into two components: (1) metabolic (maintenance) respiration, related to biomass but temperature-dependent; and (2) synthesis (growth) respiration, related to photosynthetic rate and temperature-independent. These components have not been used extensively in models simulating NPP (Hunt and Loomis 1979 modeled respiration in this way), possibly because the physiological basis for such an approach is relatively new (Thornley 1976). In the Grassland Biome ELM model, for example, aboveground respiration was solely a function of average daytime temperature (Sauer 1978).

The relationship between photosynthesis, respiration, and temperature is more enigmatic when one considers the ability of plants to acclimate photosynthetic and respiration capabilities in response to changing temperature regimes (Barbour et al. 1980). Such an adjustment factor seems much more pronounced in desert plants (Pearcy 1976), which fortunately do not constitute a major source of forage NPP in North America. However, Kemp and Williams (1980) have shown it to occur in both cool- and warm-season grasses on the shortgrass plains; forage production models may eventually consider this acclimation adjustment in simulating mechanistic responses to fluctuating climates.

Nutrients

The role of nutrients as an abiotic factor affecting NPP has received intensive research for many years, focusing first on agricultural ecosystems in terms of fertilizer responses (Black 1968). Work on nutrients and production in natural systems dealt initially with forestland, where mineral cycling can be closely monitored (Tennessee Valley Authority 1968, Likens et al. 1977).

Forage production on pastureland in relation to mineral nutrient supplies received extensive investigation in Great Britain, Australia, and New Zealand before comparable research commenced in the United States (Snaydon 1981, Till 1981). Review papers on the role of nutrients as they affect forage NPP in the United States have been written by Wight (1976) for the northern Great Plains, Jones and Woodmansee (1979) for the California annual grassland, and West and Skujins (1977) for the Great Basin. Adams and Stelly (1962) examined fertility requirements for southeastern species.

These and other papers demonstrate that interactions between mineral nutrients and plant production are complex and difficult to generalize. The synergistic effects between nutrients and other environmental factors often overshadow the direct production response, thereby making mechanistic model building a complicated task. One of the few research efforts involving a holistic approach to describing forage production resulting from variations in nutrient levels and soil water took place on the shortgrass prairie (Dodd and Lauenroth 1979). The authors found increases in aboveground NPP to be by a factor of 2 in response to augmented nitrogen alone, and by an order of magnitude when the fertilizer effect was coupled to additional soil water (fig. 4).

Soil Water

As previously stated, soil water availability can have a substantial influence on variation in forage production, especially where water frequently limits the rate of photosynthesis and leaf growth. Leaf growth has been shown to be one of the processes most sensitive to water stress (Chu and McPherson 1977), and several re-

searchers have pointed out a positive correlation between allocating photosynthate to leaf area development and increased productivity (Christie 1975). There are more implications to the water factor, however, than short-term fluctuations in growth. Protracted effects and interactions are also important.

The long-term consequences of drought on range forage plants can affect NPP under certain conditions for years after precipitation has returned to normal. For example, in a review of drought effects on northwestern ranges, Bedell (1980) showed that recovery of forage NPP is closely tied to past grazing use (i.e., a climate/animal interaction exists). He related lack of restoration of production to decreased carbohydrate reserves and root growth.

The response of vegetation to mechanical land-treatment practices that enhance water availability, such as furrowing, ripping, pitting, and waterspreading, can cause large increases in forage NPP within localized areas, if conditions are suitable (Vallentine 1980).

Other Soil Factors

Each of the factors discussed above (i.e., climatic factors, nutrients, and soil water) are variables known to be significant in predicting NPP dynamics on a given

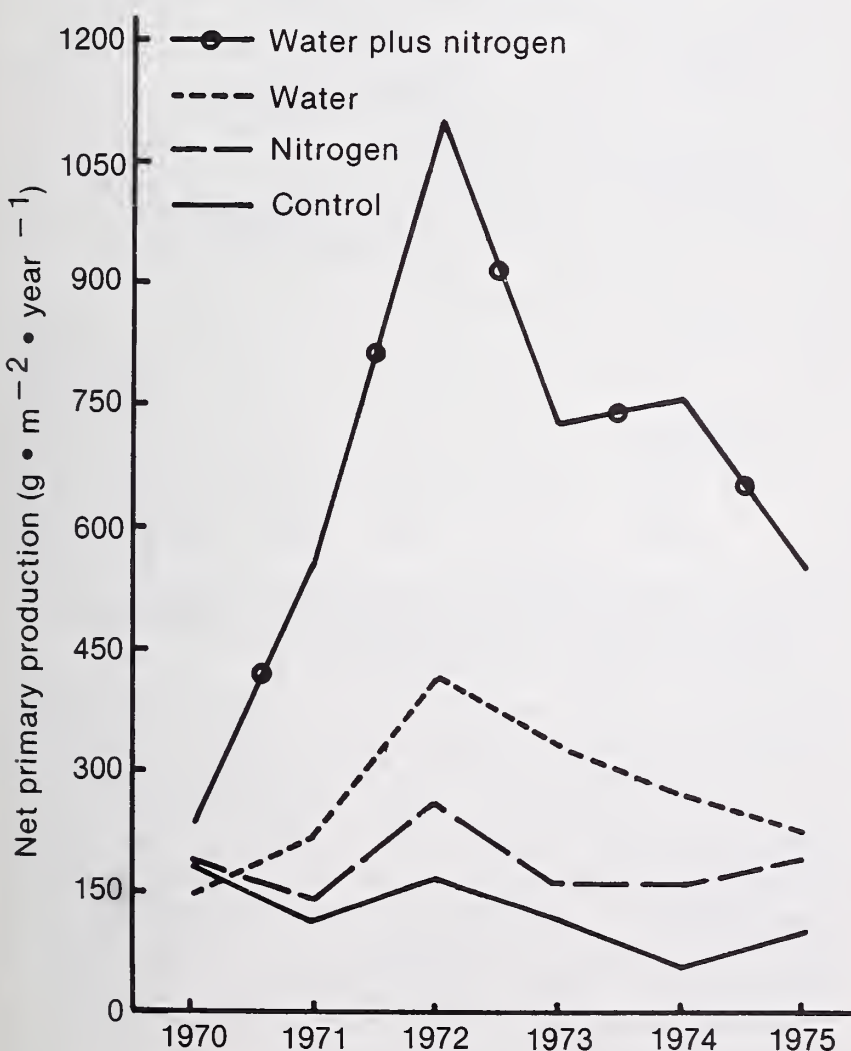


Figure 4.—Aboveground net primary production for water and nitrogen stress experiment, 1970-1975, shortgrass prairie community, Colorado. (Adapted from Dodd and Lauenroth 1979.)

site. In great part, each affects production by the way it modifies the state of the soil system, both from site to site and for a given site over time. These factors are the principal ones used in predicting forage production.

Plants do not respond solely to climate, nutrients, and water, however. Production is related to the total soil system, including a myriad of physical properties that vary spatially across the landscape. Insights into this complex relationship between forage production and soil properties have developed rapidly during the past 30 years.

Concepts fundamental to understanding the connection between forage production and the soil have been outlined in a notable paper by Shiflet (1973). He defined range site as "a distinctive kind of rangeland which differs from other(s)...in its ability to produce a characteristic natural plant community...based on differences in kinds or proportions of plants making up the climax community or differences in productivity." Shiflet (1973) related the following theory based on the idea of a range site:

- (1) more than one specific soil (defined here as a series or phase of a series—see Soil Survey Staff 1980) may support a single range site; however,
- (2) a single soil should not support more than one range site.

Consequently, from an ecological perspective, any techniques for evaluating ecosystem forage production must consider basic soils information. At the local level, good correlations may be obtained between forage NPP and the soil series category of classification or phase of series (Shiflet 1973).

Regional forage production analysis procedures, in contrast, will not be able to make use of detailed soils properties because of problems associated with keeping track of the tremendous number of soil series in the United States (approximately 12,000 at last count). Although no soil/plant production research comparable to that dealing with range sites has taken place at the regional level, one should expect the same concept to hold, but at a lower resolution associated with higher categories of soil classification (Heerwagen and Aandahl 1961). The soil family, for example, groups soil series having similar chemical and physical properties that affect their response to management (Soil Survey Staff 1975). It may be necessary to use even higher soil classification categories, such as subgroups or great groups, as a classification base for regional forage production models. Nonetheless, the plant-soil relationships still must be considered.

Fire

Fire, as an abiotic factor, influences forage production in several different ways, mostly beneficial. On forestland, fire can remove the overstory canopy, thereby allowing increased light into the understory. On other rangeland ecosystems, fire can be used to control unpalatable shrubs, eliminate thick litter and standing dead layers, provide increased levels of available ash

nutrients, and increase nitrogen by stimulating soil bacterial mineralization rates (Sharrow and Wright 1977). The new growth following fire is more palatable to both livestock and wildlife. The species composition of forage can be enhanced following fire to provide increased forbs and palatable, available browse through resprouting.

In general, the detrimental effects of fire on forage production are not serious enough to counteract beneficial ones. Some forage species cannot tolerate the high temperatures found in many fires, resulting in high mortality (Daubenmire 1968); a good example of such a species is *Festuca idahoensis* (Blaisdell 1953).

Specific responses of forage production to fire in various regions of the country have been documented in numerous publications. For example, Wright and Bailey (1980) have written an excellent review of the literature on fire ecology in the Great Plains in which dynamics of both species composition and production on the tallgrass, mixed-grass, and shortgrass prairies are synthesized. Wright (1972, 1978) also reviewed the literature on forage response to fire in shrub communities throughout the United States and in the Rocky Mountain ponderosa pine zone. Lewis and Harshbarger (1976) discussed effects of burning in the Southeast.

The responses of forage species to fire, as expected, are affected by interactions with other environmental factors. For example, in the Southeast, Duvall (1962) found that differential grass production on burned versus unburned pastures depended greatly upon grazing intensity; on closely cropped pastures, other factors, such as increased light, compensated to provide increased growth (fig. 5).

In a simulation of prescribed burning impacts on the tallgrass prairie, Parton and Risser (1980) predicted that triennial spring fires would increase NPP by 9% to 10% while decreasing the amount of litter, production of cool season plants, and nitrogen balance. The authors further concluded that annual burning would have the short-term benefit of increasing NPP even more, especially on grazed pastures, than burning once every 3 years; however, its long-term effect would result in decreased NPP because of greater nitrogen losses.

Effects of Animals on Forage Production

An initial approach towards developing a model or other technique to predict forage production might logically be to consider grazing and browsing animals only as receivers of energy in terms of secondary production. Feedback mechanisms of the grazing animal affecting NPP, under such conditions, would receive little attention. In fact, however, the primary consumer can have a substantial influence on forage production, both directly and indirectly. Moreover, in terms of plant response, the effect may be either negative or positive (or both), depending upon the situation.

Until the 1970's, the prevailing belief among ecologists and range scientists was that grazing only suppressed NPP of forage plants by removing photosyn-

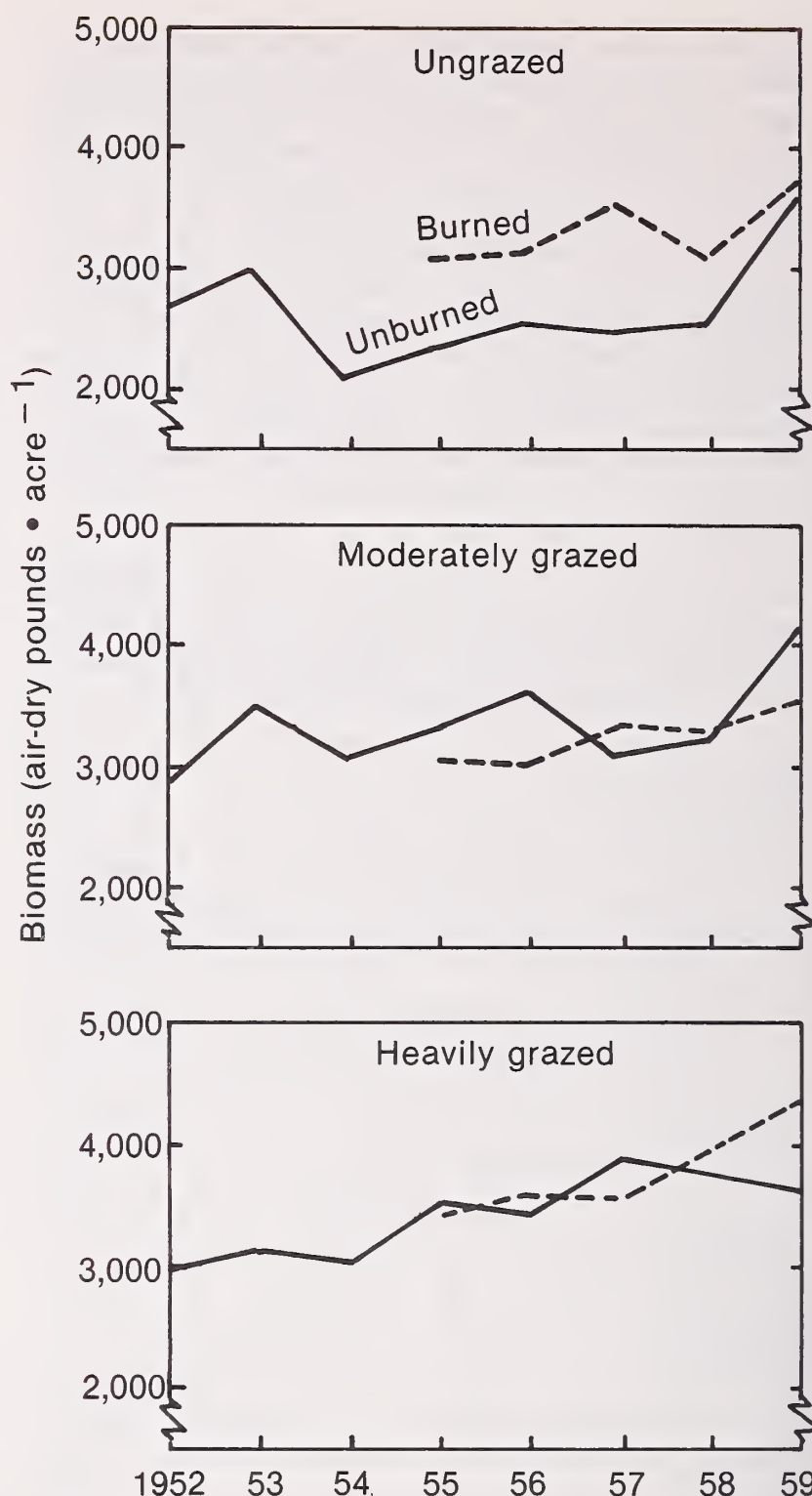


Figure 5.—End-of-growing-season biomass of Louisiana *Andropogon* grassland under three grazing intensities with and without burning. (Adapted from Duvall 1962.)

thetic tissue. The mechanisms for long-term decreased growth under these conditions were shown to be related to decreased vigor (Johnson 1953) resulting from a loss of carbohydrate reserves, which made preferred (i.e., defoliated) forage plants less competitive, especially during the critical, early spring growth period (fig. 6) (Cook 1966). To a lesser extent, early heavy grazing can also be detrimental to forage growth by causing a reduction in plant N, which inhibits development of axillary buds of some grasses, such as *Panicum virgatum* (Beaty et al. 1978). In 1963, Jameson extensively reviewed the literature relating to how plants respond to foliage removal, but his paper pertained only to the ways NPP is reduced by grazing.

A recent paper (Lacey and Poolen 1981) summarized the results of 12 previous studies evaluating the response of herbage production to moderate grazing. Its authors demonstrated empirically that moderate grazing suppressed NPP in almost every case, by an average of more than 30%, if the studies are considered collectively. They concluded, however, that ungrazed pastures would not continue to increase in relative forage production if nonuse persisted beyond 4 to 7 years, the time frame of the studies upon which they reported.

Ultimately, forage production on rangeland also decreases in response to grazing pressure by changing community species composition. Such a process, called retrogression (Stoddart et al. 1975), was recognized and described very early in the history of ecology (Sampson 1919) and led to the concept of range condition based on classification of forage plants into three categories—decreasers, increasers, and invaders (Dyksterhuis 1949). Plants increase or decrease in abundance primarily in response to differential grazing pressure resulting from forage preference or selectivity. The literature on forage preference and its quantification have been reviewed by Krueger (1972) and Arnold (1981). The classical relationship between the abundance of decreasers, increasers, and invaders is depicted in figure 7. Consequently, the ecosystem process of energy flow, regarding NPP of forage plants, is tied closely to the synecological concept of successional state.

Few of the ecosystem models developed to simulate energy flow consider a successional-varying vegetation state, except in terms of arbitrary abundance units (Bledsoe and Van Dyne 1971). Whittaker (1975) reported

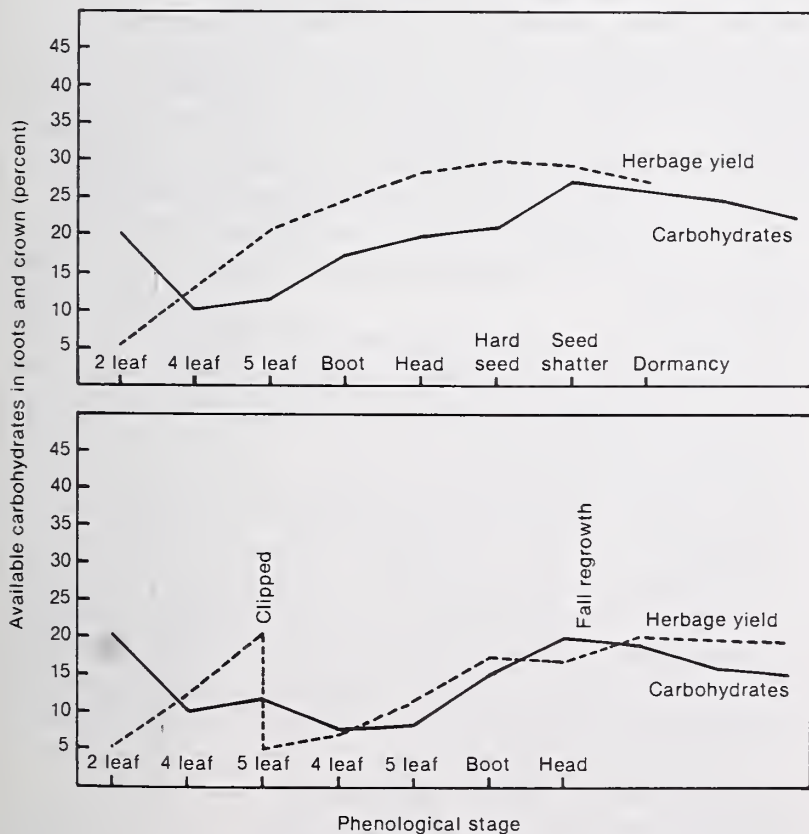


Figure 6.—Carbohydrate balance and herbage yield of a typical grass during its phenological development—(A) unaffected and (B) as affected by clipping. (Adapted from Cook 1966.)

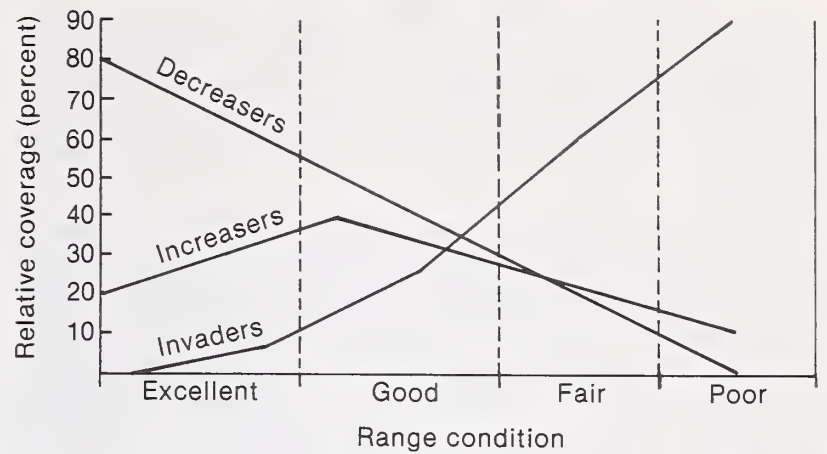


Figure 7.—Proportional relationship among decreasers, increasers, and invaders as range condition goes from excellent (i.e., climax or near-climax) to poor condition (pioneer community). Note that invaders are not part of the climax community. (Adapted from Dyksterhuis 1949.)

on an unpublished study by Holt and Woodwell, on the Brookhaven forest of New York, that predicted total NPP during succession (fig. 8), and Kellomäki et al. (1977) used a modeling approach to estimate annual production of *Vaccinium* spp. in response to succession in Finland. Other than these, little has been reported.

The literature on the theoretical relationship between productivity and succession has been reviewed by Odum (1971). He postulated that net community production should approach zero, because of the convergence of gross production and respiration rates, as a community nears climax (fig. 9). Odum's hypothesis seems better suited for forest ecosystems, with their large standing crop levels, than for rangeland, however. On rangeland, one would expect NPP of forage species to increase during succession, with a leveling at late seral stages and perhaps a slight decline at climax. The response would more likely be a function of management practices, such as grazing intensity, than of succession. In addition, the palatability and availability of what is produced must override the strict interpretation of NPP in the evaluation of this process on rangeland.

In addition to the depressant effect on NPP, grazing can act to stimulate increased forage production under some conditions. For example, warm-season rhizomatous and stoloniferous grasses of the true prairie and Southeast have increased their photosynthetic rates by up to three times as a result of close cropping, possibly because of increased crown light intensity (Beaty et al. 1977). This response is interrelated with nutrient availability, which means that the grazing factor must be considered with fire and fertilization.

Removal of shoots by grazing affects plant hormone balance, which can also result in initiation of new shoots and enhanced growth rates. Several authors (Reardon et al. 1972, Dyer and Bokhari 1976) have suggested that such growth is at least partly caused by the presence of thiamine in the animal saliva being transferred to the shoot, then translocated to the roots, where it apparently stimulates metabolic activity. Thiamine, a member of the vitamin-B complex, normally is synthesized in leaves; it has been called a root hormone, because it appears to be necessary for root meristematic devel-

opment (Sosebee 1977). Other recent experimental evidence, however, supports the null hypothesis that saliva from grazing animals either contains no growth regulators or, if hormones are present, does not stimulate top or root growth or tiller production (Detling and Dyer 1981).

Although the interactions between NPP of forage plants and the herbivores that feed upon them are complex and difficult to describe, much less quantify, field experiments do support the hypothesis that grazing can stimulate forage plant growth. For example, Vickery (1972) found NPP of a pasture in New South Wales, Australia, to be greater at a stocking rate of 20 sheep per hectare than at either 10 or 30 sheep.

Generalizations on the interactive relationships between NPP and forage utilization are tenuous; nonetheless, some judgments are possible. First, on an overall basis, herbivory tends to have a negative effect on plant growth, reproduction, and survival. Second, even if clipping warm-season sodgrasses enhances NPP under the right conditions (Hazell 1965), such is not the case for cool-season bunchgrasses (Wilson et al. 1966), especially in xeric environments (Cook et al. 1958). Clipping also depresses NPP of forbs (Julander 1968). The effects of browsing on shrubs have received less attention than have grazing effects on grasses, but the available evidence reinforces the same general response. Browse growing in moist environments appears to be somewhat stimulated by a reasonable level of utilization at certain phenological states (Lay 1965), but desert shrubs decrease in NPP under the influence of browsing (Cook 1971).

Belowground consumers (i.e., micro and macroarthropods, nematodes, etc.) have been the subject of only a small fraction of the total research effort into herbivory as a process affecting NPP or other ecosystem functions. Nonetheless, evidence exists that belowground herbivores may consume more biomass than those aboveground (Coleman et al. 1976). The loss of roots and other belowground plant material to consumers may even impact upon aboveground NPP to a greater degree than might be expected from its own magnitude (Chew 1974). For example, a recent laboratory study (Detling et al.

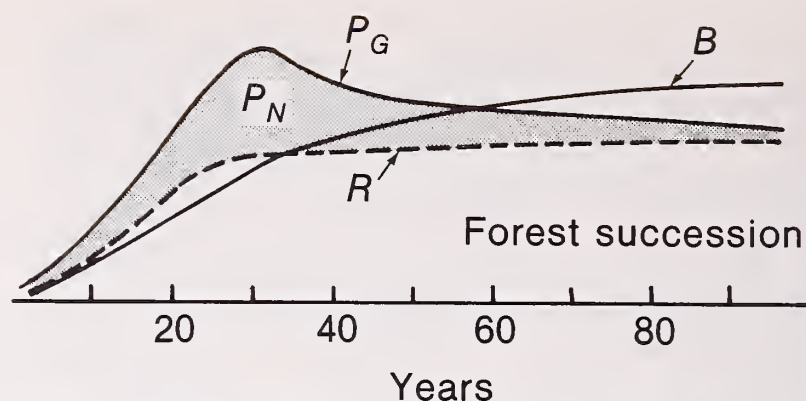


Figure 9.—Net community productivity (P_N =shaded area) of a forested ecosystem in relation to gross community productivity (P_G), respiration (R), and biomass (B) during succession. (Adapted from Odum 1971, originally published in Kira, T., and T. Shidei. 1967. Primary production and turnover of organic matter in different forest ecosystems of the western Pacific Japanese Journal of Ecology 17:70-87.)

1980) demonstrated that crown and leaf biomass of *Bouteloua gracilis* decreased approximately 20-25% following a moderate degree of root clipping, primarily in response to a 50% reduction in tiller production and increased carbon allocation to the clipped roots.

From a resource management viewpoint, the importance of belowground consumer-forage NPP relationships is questionable because abundance levels of the former are extremely difficult to monitor, much less manipulate. Perhaps much of the difficulty in using such relationships to predict NPP will result from this inventory problem.

Influence of Land Management and Use on Forage Production

In the past 100 years, humans have increasingly become manipulators of ecosystems rather than merely creatures in them. For this reason, a discussion of their ability to control forage production is appropriate. Although the question of land use may be more properly an economic one, it does have ecological implications.

The production of forage within a given area can be modified by land managers and other decision makers in different ways:

1. Production can be increased by altering the environmental factors affecting plant growth, such as water (irrigation), nutrients (fertilization, fire), and light (harvesting, fire).
2. Forage production can be increased by causing a change in community composition, whereby existing species are replaced by others that are more productive, more palatable, or more usable. Such alterations can result from management on an agronomic basis (plowing and seeding) or an ecological basis (using range management techniques to shape the direction of natural succession or retrogression). Moreover, such replacements of community composition with more productive forage species are frequently a spinoff from other management objectives (e.g., noxious weed control, improvement of riparian habitat, forest harvest practices).

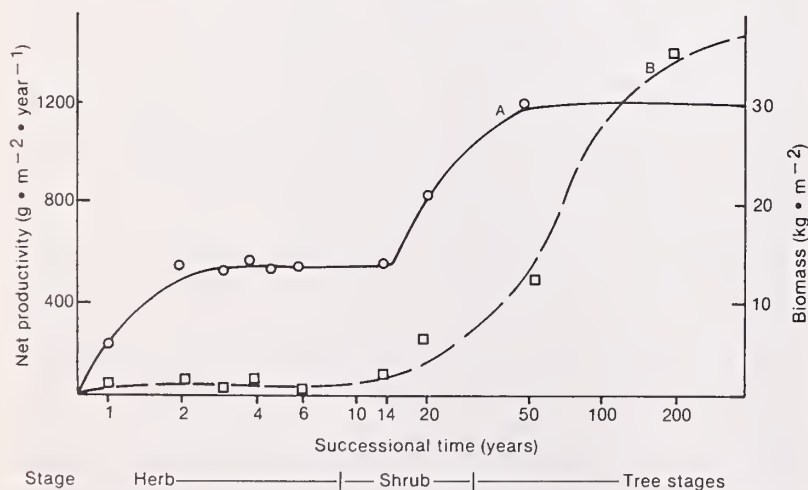


Figure 8.—Net primary productivity (A) and biomass (B) during succession in the Brookhaven oak-pine forest, New York. (Adapted from Whittaker 1975, originally presented in B. Holt and G. Woodwell, unpublished.)

3. Effective forage NPP can be increased by using management tools to make what is produced more available. In this case, actual productivity is not altered, but the amount of biomass available for consumption by grazing animals increases. Range managers have accomplished this by using grazing systems to concentrate livestock, which causes more uniform levels of utilization within a pasture, and by implementing range improvements to create primary range out of secondary range. Primary range is that part of the suitable range that livestock naturally prefer or, under management, will use first. Normally, it is readily accessible and has available water. Ordinarily, primary range areas will be grazed to allowable levels or be overused before other parts of the range are used to any great extent. Secondary range is that part of the range that is suitable for livestock use but is used very little or not at all because of lack of accessibility, lack of water, management system, or a combination of these. It should be noted that grazing systems, if successful, often serve the dual purpose of increasing actual forage NPP through succession and effective production as outlined above. Improper management, obviously, can result in reductions of forage NPP through decreasing range condition (retrogression) and grazing programs that allow ineffective utilization.

4. The available amount of forage produced within a given area can be significantly reduced or increased by changes in land use. The use of rangelands for livestock production is, perhaps, the most extensive form of land use, with the possible exception of dispersed recreation. Shifts and growth in populations have led to a creeping encroachment onto range and pastureland by suburban growth, expanding transportation systems, and other forms of more intensive land use (Love 1970). This loss of forage production could be somewhat offset by shifts from cropland and forests to pastureland.

The first of these four areas, altering environmental factors, has already been discussed. The others require further elucidation.

People involved in grazing systems and range improvements have gathered a wealth of experience; however, few generalizations have been published or are generally available. Van Poollen and Lacey (1979) concluded that, on an overall basis, forage production increased 13% when grazing systems rather than continuous grazing were used, and approximately 30% when grazing intensity decreased for a given system. Variations were large among the various grazing regions in the United States, however. They varied from large increases in the Pacific Northwest and Texas Rolling Hills to no significant difference (or actual production losses) in the northern and central Great Plains (fig. 10).

In another review, Herbel (1971) found grazing systems to be detrimental in the California annual grassland and only moderately effective in the Pacific bunchgrass region. He hypothesized that improvement of bunchgrasses depends on their restoration of vigor

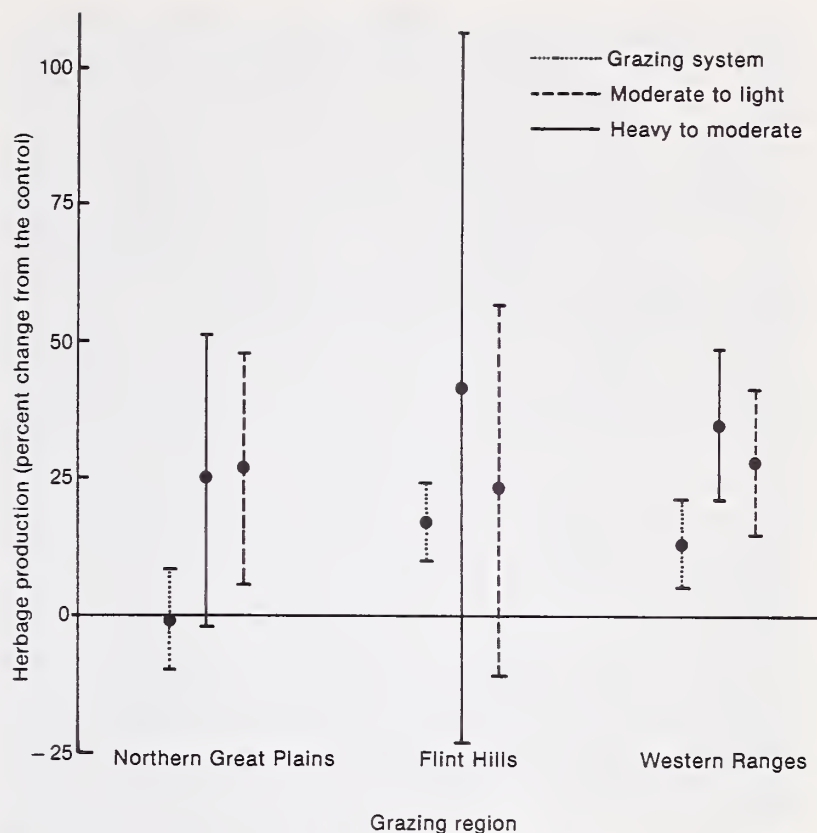


Figure 10.—Response in herbage production for two grazing regions and the western ranges under change in grazing system (from continuous use to rotation system) and grazing intensity (heavy to moderate, moderate to light). Brackets indicate 95% confidence interval. (Adapted from Van Poollen and Lacey 1979.)

and ability to produce seed. The concept of rest-rotation grazing systems has been explained by Hormay (1970).

The response of forage NPP to range improvements is extremely varied and unpredictable. It is a function of several variables, including the kind of improvement, site factors, climate, and initial vigor of the desirable forage species. On a given site, the response to specific range improvements has historically been ascertained by field experiments. Aside from predicting responses from fertilization and irrigation, little in the way of modeling has been accomplished in this area. Moreover, within localized areas, the effects of range improvements can be profound. For example, Hull and Klomp (1974) reported a threefold increase in crested wheat-grass production after sagebrush control in southern Idaho (fig. 11).

On a regional or national basis, however, the influence of range improvements on forage production has been handled more suppositionally, often being based on expected long-term trends of livestock. A potential notable exception is the Grant County (Oregon) Evaluation Study, a 10-year federal, state, and private cooperative program designed to ascertain, among other goals, the long-term effects of improvements on forage production, at least for the Blue Mountain region. This carefully designed project may provide the necessary information to build predictive models on a regional basis. Initial results indicate that large increases, exceeding an order of magnitude, in forage production are possible under a coordinated program of range improvements² (fig. 12).

²Personal communication with Arleigh Isley, Grant County Extension Agent, John Day, Oregon.

It is unlikely, however, to expect the same level of intensive range improvements over large areas in the future, primarily because of environmental concerns and costs. Vale (1974) estimated that only 10-12% of the 40 million acres of western lands dominated by sagebrush have undergone some kind of conversion treatment to enhance grass production; further large-scale projects appear improbable because of fears that sagebrush eradication is detrimental to wildlife.

The last factor, changing land use, has been shown in the past to have the potential for creating large changes in forage production at the national level and, in some areas, the regional level. Long (1974), for example, reported on a study that showed that more than 1.6 million ha of grasslands were converted to cropland in 1974 alone. Cropland, which occupies about 25% of the conterminous United States and can be quickly converted from grassland in some areas in response to favorable market conditions, should be envisioned as the most likely repository of rangeland. Alternatively, cropland can be an important source of replacement land for natural forest and rangeland (Klopatek et al. 1979).



Figure 11.—Yields of crested wheatgrass under four degrees of sagebrush control at Holbrook, Idaho, 1965-1970. (Adapted from Hull and Klomp 1974.)



Figure 12.—Crested wheatgrass seeding in Grant County, Oregon. Forage production has been increased over 100-fold in less than 5 years. (Photo courtesy of Arleigh Isley, Cooperative Extension Agent, Grant County, Oreg.)

Other evidence indicates that land area in cropland has not significantly varied in recent years. According to Clawson (1979), U.S. cropland peaked in the 1920's at about 205 million ha and has stabilized at about 185 million ha in the last 30 years. Klopatek et al. (1979) found that vegetation types which are alterable to cropland have already been nearly completely so changed, and vegetation types that have mostly retained their natural state are least likely to undergo future changes because of rough topography or federal ownership. Both Clawson and Klopatek seem to conclude, then, that large shifts in land use are unlikely in the foreseeable future.

Schertz et al. (1980), addressing the farming outlook for this country, concurred with Clawson (1979) on the present stability of crop acreage nationally; however, he recognized that somewhat offsetting regional shifts are also taking place. Concurrent regional shifts in the U.S. range and pastureland base could significantly affect forage production potentials for the country as a whole because of differences in potential production.

The foreseeable future alluded to above by Clawson (1979) and Klopatek (1979) may extend only a short period ahead. At a recent symposium, Crosson (1979) estimated that an additional 25 to 30 million ha of cropland will be required to meet projected food demands by the end of this century, and that these tracts must come from nonagricultural instead of set-aside lands. Other sources (Dideriksen et al. 1977, Brewer and Boxley 1980) indicate that somewhere between 15 and 31 million ha of noncropland (pasture, range, forest) have a high potential for cropland development and from 14 to 37 million ha have a medium potential. Less than a million hectares, however, evidently has the potential to be quickly converted without major outlays for soil preparation or water facilities (Shulstad and May 1980).

Overall, it may be concluded that future effects of land-use conversion on forage production are not predictable, but the potential for change in either direction, given the growing world population and the international nature of agriculture and politics, is certainly feasible.

Forage Production Models

Models are, by definition, abstractions or simplifications of systems (Hall and Day 1977). Their value lies in their ability to simplify complex systems (e.g., the real world) by leaving out some information while including only those elements and interrelationships that are thought to be important in determining cause and effect. Thus, models do not represent systems completely and cannot answer all questions about the structure and function.

Characteristics of Simulation Models

In ecology, simulation models express the dynamics of ecosystems by evaluating their change of state. The state of a system is embodied in the condition of its state variables or defined components (Patten 1971). In the most common form of simulation models, the state variables are called compartments, and the model is a compartment model. The interrelationships among the state variables in compartment models are usually expressed in the form of a series of differential or difference equations. If differential equations are solved numerically (e.g., Euler and Runge-Kutta methods), as is normally done in compartment models, then little difference exists between the two mathematical forms. The system behavior is determined by simultaneously solving the series of equations. Numerical approximation solutions are used, because analytical solutions of ordinary differential equations are difficult to essentially impossible for linear equations, and impossible for nonlinear equations.

Whether or not the equations describing ecosystem behavior must be linear (i.e., being other than first degree in the case of differential equations) has been an area of controversy among ecosystem modelers. One group believes that the dynamics of natural ecosystems are ostensibly linear, even though they are driven by processes which are nonlinear (Patten et al. 1975), and that the large assemblage of linear systems theory developed in engineering which can be applied to analysis of linear models (Waide and Webster 1976) makes such an approach worthwhile.

Proponents of nonlinear models base their argument on the premise that mathematical models should be analogous to the real world system being modeled, which is generally conceded to exhibit nonlinear characteristics (Bledsoe 1976b). In addition, Innis (1975) argued that, conceptually, biologists participating in the modeling of whole systems perceive relationships in nonlinear terms; forcing the discussion in other directions would result in the loss of the contribution biologists could otherwise make. There are several inherent problems associated with nonlinear models, such as the lack of algorithms for sensitivity analysis and undesirable intrinsic characteristics (e.g., those associated with steady state) (Patten et al. 1975); however, supporters of nonlinear models believe these problems subordinate to those associated with linear models.

Models may also be classified as either mechanistic or descriptive. In mechanistic models, equations express the causality affecting each state variable's behavior; in the latter, the equations merely describe it. Systems ecologists agree that, when possible, a model should be mechanistic (Hall and Day 1977), but these models require an understanding of the autecological bases of the state variables' responses to inputs.

Models are also categorized as being deterministic or stochastic (Patten 1971). Models that produce unique outputs to a given set of initial conditions are deterministic in nature; those that produce varying outputs following some distribution of values because of some level of uncertainty are stochastic.

Special techniques, called Monte Carlo, are used to induce statistical variations in simulation models (Breipohl 1970). Using Monte Carlo techniques in simulation models often requires a substantial amount of computer time. Kowal (1971) has stated that, in the case of linear deterministic models, probabilistic inputs have a good potential for imitating dynamic ecosystems. Because of their applications in electrical engineering (i.e., "noise" and "random signals"), linear deterministic models are well validated.

Forage Production Models

Early forage production models were simple, descriptive, and deterministic in nature (Clary 1964); however, more elaborate models predicting primary production have been developed in recent years. Van Dyne et al. (1978) has indicated that models are related to the hypotheses being addressed by it (i.e., hypotheses concerned with natural resource management must be specific to the particular ecosystem(s) involved). Such hypotheses are developed by experienced scientists, based on their own backgrounds and knowledge of the literature. Models so developed, for example, might be able to address hypotheses on forage production as affected by grazing intensity and season of use, insect outbreaks, irrigation, fertilization, fire, and range improvements (Van Dyne et al. 1978).

An interdisciplinary strategy, such as described by Van Dyne (1966), has been shown to be necessary to accomplish the kinds of goals that go with a modeling approach to describing dynamics of natural systems. Interdisciplinary techniques require the use of a common vocabulary and a high level of coordination among team members.

According to a recent Forest Service problem analysis (USDA Forest Service 1981), the state of the art in ecological analysis is currently best expressed in terms of either interdisciplinary teams (Delphi process) or simulation models, with models holding the most promise for predicting impacts of resource management on forage NPP, as well as other resource outputs. A brief review of representative ecosystem models used in estimating forage production is given in table 1. Van Dyne and Abramsky (1975) provide another overview of models simulating ecosystem productivity. In addition,

Table 1.—Listing of recent simulation models in which forage production is an integral component

Reference	Type of model	Inputs and/or driving variables	Remarks
1. Kelly et al. (1969)	Seven-compartment model of NPP ¹ of <i>Festuca</i> and <i>Andropogon</i> .	Growth is a function of available solar energy based on a sine function.	Primarily this model was designed to simulate transfer of biomass to roots, standing dead, and litter, once NPP had "occurred."
2. Ross et al. (1972)	Simplified model of grass-legume sward.	Growth of legume based on light intensity in canopy and growth of grass upon both light intensity and available N.	Potential photosynthesis nonlinear functions of light intensity and LAI ² growth expressed in terms of LAI.
3. Singh (1973)	Six-compartment linear model of herbage dynamics of tropical grasslands.	Total production based on time-varying transfer coefficients.	See remarks for Kelly et al. (1969). Model structure is very similar.
4. Bledsoe (1976a)	Total systems model (PWNEE) with some 40 state variables. Based on first-order, ordinary, nonlinear differential equations.	NPP is a result of equations for photosynthesis, translocation, respiration, and death. Photosynthesis is a function of light intensity and duration, temperature, soil water, nutrient supply, and tissue aging.	One of first models in which primary production is based on mechanistic parameters. Site specific to the shortgrass prairie.
5. Noy-Meir (1978)	Simple model of primary and secondary production in a seasonal pasture based on system of linear differential equations.	Plant growth rate is a linear function of biomass less respiration.	Equations are simple enough to allow for exact analytical integration.
6. Brockington (1978)	Model of sward production based only on soil water deficit at two levels (topsoil and subsoil).	Soil water deficit is a function of meteorological data for rainfall, irrigation, and potential evapotranspiration.	Soil water deficit is the stress beyond field capacity.
7. Sauer (1978)	Submodel of primary production as part of total systems model (ELM) of the North American grasslands biome. About 30 compartments depicting carbon flow through warm and cool season grasses, forbs, shrubs, and cactus. ELM is nonlinear and based on difference equations.	NPP is equal to GPP ³ less respiration. GPP is a function of soil water, air temperature, nitrogen, phosphorus, light intensity, and phenology. Other factors determining biomass dynamics of primary producers include grazing, translocation, and death.	ELM is similar to PWNEE (Bledsoe 1976a) as a mechanistic model. It is somewhat more suitable for general use because it utilizes a simulation language (SIMCOMP) ⁴ rather than FORTRAN, with parameters for several grassland types instead of being specific to the shortgrass prairie.
8. Cale (1979)	This model (LINEAR) is a total systems model of the shortgrass prairie similar to PWNEE (Bledsoe 1976a) except for a greater number of belowground and lesser number of aboveground state variables. LINEAR is based on a system of time-varying linear differential equations.	NPP is assumed to be 66% of GPP. GPP is a function of light intensity and duration, temperature, and evapotranspiration.	LINEAR was originally developed as a class project (Patten 1972) to show that a linear model could accurately predict biomass dynamics of a shortgrass ecosystem. The IBM simulation language CSMP was used in this study.
9. Detling et al. (1979)	Intraseasonal model of blue grama production. Contains 14 compartments. Mechanistically simulates carbon allocation in early spring (from crown) and later (from leaves).	Carbon flow is a function of temperature, soil water, light, and nitrogen.	Designed as an improvement to Sauer's (1978) producer submodel in ELM (see above).
10. Irwin and Peek (1979)	Regression model of shrub production following logging in a closed forest of the northern Rockies.	The regressions predicting production are based on time since tree removal and overstory remaining.	This model was designed to couple with a timber growth model titled PROGNOSIS (Stage 1973).

Table 1.—Listing of recent simulation models in which forage production is an integral component—Continued

Reference	Type of model	Inputs and/or driving variables	Remarks
11. Fick (1980)	Pasture production submodel (CANPAS) of a whole farm simulation model. CANPAS is a differential equation model with six compartments.	Equation simulating NPP is a function of potential NPP and the difference between a ceiling biomass and an actual biomass. Potential NPP is related to six abiotic and biotic variables.	The model predicts yield from a series of 16 differential equations. The CSMP simulation language is used.
12. Grant and French (1980)	A model designed to simulate the functional role of small mammals in grassland ecosystems. Composed of three submodels, one titled "Biomass." Biomass sub-model has 12 state variables.	NPP is a function of soil water, topsoil N, temperature, and small mammal activity.	The model is based on difference equations and makes use of the SIMCOMP simulation language.

¹NPP is net primary production.

²LAI is leaf area index.

³GPP is gross primary production.

⁴For a discussion of SYMCOMP, see Innis and Gustafson (1978).

Van Dyne³ has summarized models used in simulating animal production systems.

Because there have been no models explicitly designed to predict regional forage production on the basis of abiotic driving variables, the mechanisms necessary to do so on such a large scale are not known. It is logical to expect, however, that regional models will be of relatively low resolution and will rely heavily on seasonal precipitation patterns as a driving variable. Wysong and Fisser (1974) published statistical models describing perennial grass production in western Wyoming, in which spring precipitation and the previous year's winter-plus-spring precipitation accounted for the most variation in production. Other important factors, especially on drier sites, were depths of the A-horizon and root zone. Modeling appears to offer the best long-term approach to attaining the integrated socioeconomic-level information required for regional and national resource planning. It may well be in this area that opportunities to advance the state of the art will be most beneficial.

Forage Production as a Factor in Secondary Production

Animals must obtain from food all of the chemical compounds necessary to sustain life and carry out their metabolic needs. The concept of trophic levels and food chains, which explains this process in ecosystems, has been an accepted principle of ecology and energetics for many years (Lindeman 1942); nonetheless, the uptake and turnover of energy at secondary levels is not yet clearly understood (Darnell 1968). In the 1970's, the situation started to change, primarily as a spinoff of expanding research on the analysis of primary production. The International Biological Program (IBP) provided impetus to this effort, especially for nondomesticated animals (Scott et al. 1979).

³Systems analysis in analysis of animal production systems. Invited paper on modeling for IV World Conference on Animal Production. Buenos Aires, Argentina. August 1978.

The relationship between livestock production and the quantity and quality of available forage has received detailed study for the past 30 years. For the most part, however, this level of knowledge has not been used in range management at state or federal levels; nor has there been a requirement to do so, because the "standard" product of the range is an animal unit month, which has been assumed to be the same, regardless of the variables affecting its worth.

On federal lands the price of an AUM is constant regardless of the value of the forage. Factors which should affect forage value are numerous, but include quantity, quality (primarily protein concentration), topography, distance from water, distance from roads and other grazing lands, presence of predators or poisonous plants, and improvements. On private lands, such variables are generally accounted for in the market price. It is beyond the scope of this paper to examine the AUM and secondary production in detail; nevertheless, a brief overview of the relationships between forage quantity (energy) and forage quality in comparison to secondary production (particularly red meat production of livestock) is appropriate.

Energy Requirements of Grazing Animals

As previously discussed, ecological efficiency of ecosystems relates to the efficiency in which solar radiation is fixed by autotrophs, and, thereafter, transferred to herbivores and carnivores.

Energy taken in by foraging animals is used for maintenance, weight gain, milk production, fetus development, hair and wool growth, and respiration (Cook 1970). Efficiency of conversion at the consumer level involves the integration of numerous genetic, physiological, and environmental factors.

Energy intake by grazing animals has been divided into several components (Cook 1970). Gross energy is the

energy value (calories) of ingested forage. Part of this energy remains undigested and is excreted from the animal after passing through the alimentary tract. That which becomes digested is termed digestible energy. If energy losses in the form of urine and methane (gas) are subtracted, the remainder is termed metabolizable energy. Deleting energy lost in heat of respiration, which varies according to activity level, workload, etc., leaves a remainder called net energy. Net energy defines the level of energy available to the animal for body maintenance (replacing cells that die) and secondary production.

From an energetics viewpoint, secondary production in grazing or browsing animals includes production of red meat, fat, bones, milk, and wool (Cook 1970). This somewhat contravenes the colloquial delineation of red meat production often used in range management.

The use of digestible energy as a measure of energy content of forage is useful in a feedlot situation; however, in a rangeland ecosystem, such a measure can overestimate available energy. Many range plants, especially browse species, are relatively high in essential oils and fats, which tend to be digested but eliminated in the urine. Consequently, metabolizable energy is deemed to be more suitable than digestible energy (Cook 1970). For example, Cook and Harris (1968), in a study of nutritive value of seasonal range plants, found forage species on desert winter ranges to be somewhat lower in gross energy (4,370 versus 4,125 kcal·kg⁻¹) than those on seeded spring range and summer range. Moreover, less of that energy (39% versus 48%) represented metabolizable energy. Van Dyne (1969) reviewed the literature on the techniques for determining the energy content of forage plants.

To develop an energy budget model for secondary production of grazing or browsing animals, one must know the energy requirements for various metabolic activities (e.g., maintenance, activity, fetal growth, body gain, wool growth, respiration). Cook (1970) provided an excellent review of the literature on this subject. Of course, the animal response to forage energy cannot be described without a reminder that other important plant nutrients can also limit secondary production. These include digestible protein, phosphorus, and carotene (Cook 1970). Perhaps the most important of these is protein.

Protein Requirements of Grazing Animals

About 80% of the atmosphere is composed of nitrogen. Despite the presence of such vast quantities of nitrogen, most plants and all animals cannot metabolize N₂ directly, but rely upon its fixation by microorganisms into usable inorganic form. Because of limited nitrogen availability, productivity at both the autotrophic and primary consumer trophic levels is constrained by nitrogen in many situations. This section examines the relationship between forage quality (defined here in terms of protein content) and secondary production of grazing animals. To comprehend the factors controlling this

interaction, one must first examine the nitrogen cycle as it affects the level and form of nitrogen in forage plants. The influence of nitrogen on the amount of available forage (i.e., NPP) has been previously discussed.

A clear overview of the generalized nitrogen cycle is in the elementary soils text by Brady (1974). Most research into nitrogen dynamics has been conducted on agronomic systems, which tend to be simpler and more completely understood than natural systems. In the last decade, however, several investigators have traced the pathways of nitrogen in natural terrestrial ecosystems, including deserts (West and Skujins 1977) and grasslands (Reuss and Innis 1977, Woodmansee 1978, Jones and Woodmansee 1979). Rodin and Bazilevich (1967) have presented data on numerous ecosystems.

Research has demonstrated that the four plant nutrients most crucial to secondary production of range livestock are protein, phosphorus, energy, and carotene. Of these, the proportion of digestible protein appears to regulate animal gain more closely than any other factor (Cook and Harris 1968). Digestible protein is the protein in consumed feed apparently digested by the animal. Dietz (1970) reviewed different measures of forage quality and their definitions. In relating secondary production to forage quality, one must consider more than just nitrogen levels because of variations in nitrogen digestibility among species, in plant parts, and with time. Crude protein is commonly defined as nitrogen content of forage dry matter multiplied by 6.25; however, nitrogen digestibility varies with several factors, primarily tissue age (Cook and Harris 1968). The percent digestible protein in forage plants varies widely. In general, diets of range livestock in spring contain about 7-11% digestible protein, while, in the fall, this figure declines to 4% or less (Cook et al. 1977). On winter sheep ranges of the Intermountain region, digestible protein can dip below 2% (Cook and Harris 1950).

Not only does digestibility of forage protein decrease with tissue age, but the actual levels of nitrogen, which determine crude protein, decline also, primarily as a result of translocation (fig. 13). This effect is more pronounced in grasses than in browse, probably because nitrogen is translocated to the crown and roots of grasses, while in browse some nitrogen may be stored in the twigs and remain available for consumption.

The compounded net result of decreasing crude protein and its digestibility during a growing season can have a profound effect on secondary production once minimum thresholds are not met. Vavra and Phillips (1980) followed the diet quality of cattle and their resultant change in weight through several grazing seasons on summer range in northeastern Oregon. They found significant fluctuations from year to year, probably because of precipitation pattern influences; nonetheless, in general, crude protein of forage consumed decreased continuously and somewhat proportionally to the nitrogen level of principal forage grasses (fig. 14). In contrast, cattle weight gains maintained a somewhat constant rate for most of the grazing season, ostensibly until forage quality did not meet the animals' minimum needs, after which it dropped rapidly (fig. 15).

Cook et al. (1977) evaluated the response of range animal weight gain to changing digestible protein content of forage, and found an exponential relationship for both cattle and sheep over all seasons of use (fig. 16).

Cook and Harris (1968) proposed recommended levels of energy and digestible protein for range livestock (table 2). If one assumes a digestibility of 70% of the forage consumed in the Oregon study (Vavra and Phillips 1980), the point at which their cattle weight gains started to rapidly decline is in reasonable agreement with the recommended minimum protein level.

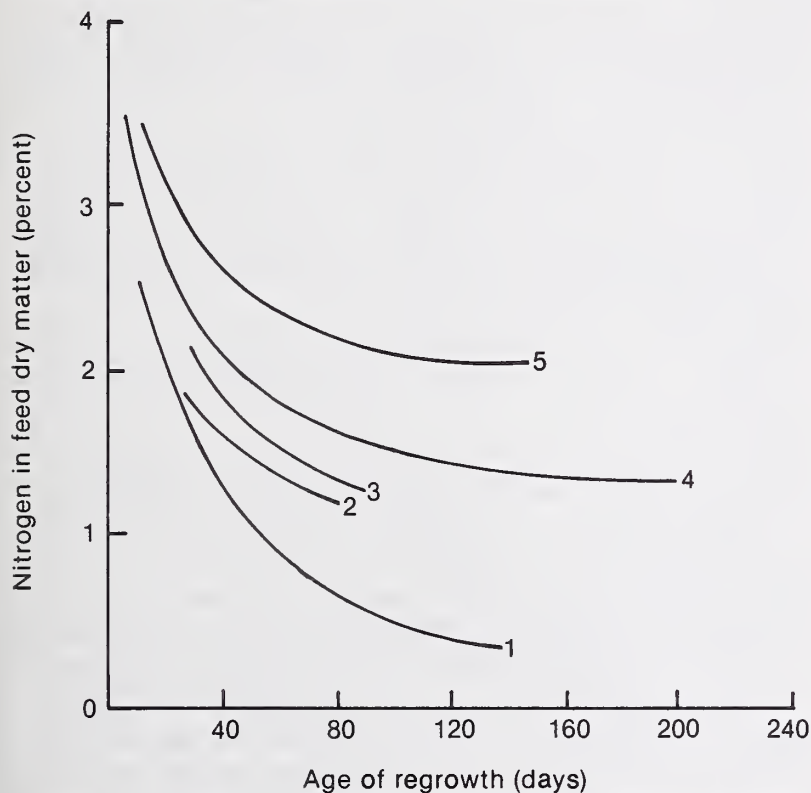


Figure 13.—Effects of age on nitrogen contents of several tropical grasses: 1. *Digitaria decumbens*; 2. *Chloris gayana*; 3. *Setaria* sp.; 4. *Sorghum aluum*; 5. *Pennisetum clandestinum*. (Adapted from Simpson and Stobbs 1981.)

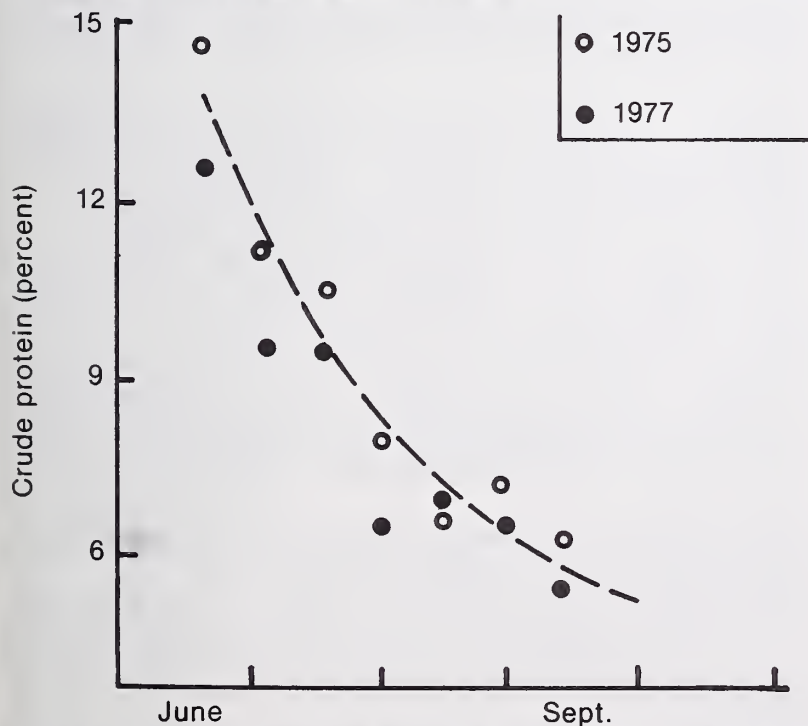


Figure 14.—Crude protein in cattle diets during 2 years for the summer grazing season in the Blue Mountains, Oregon. (Adapted from Vavra and Phillips 1980.)

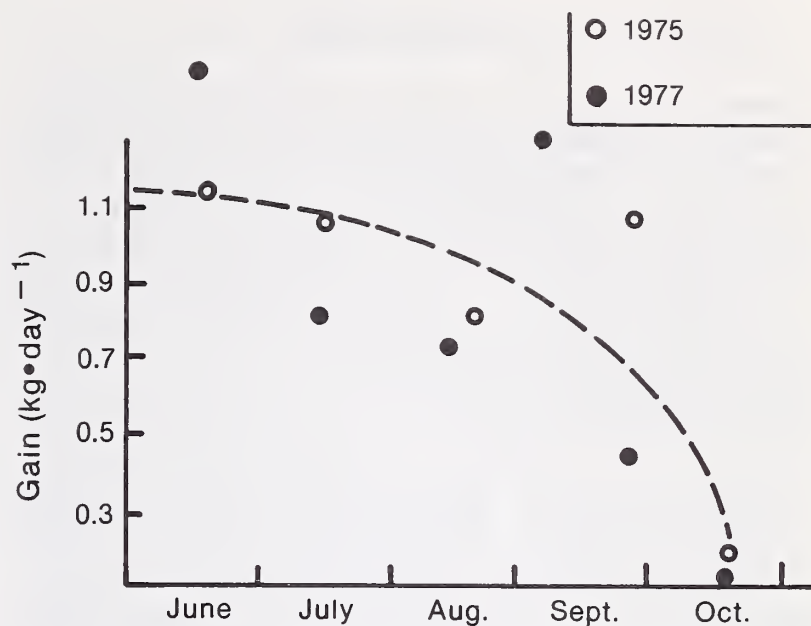


Figure 15.—Average daily weight gain of calves during 2 years for the summer grazing season in the Blue Mountains, Oregon. (Adapted from Vavra and Phillips 1980.)

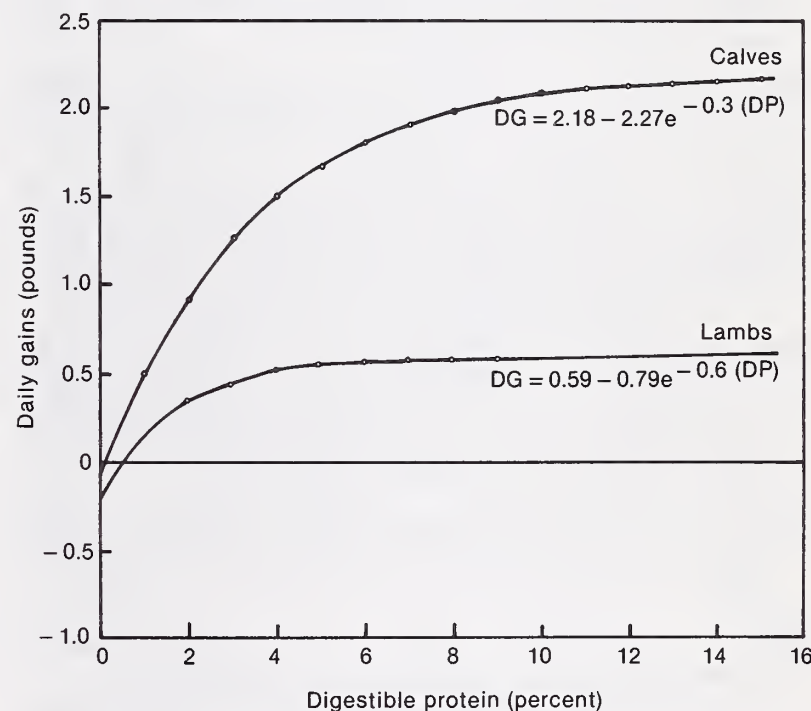


Figure 16.—Predicted average daily gain for range calves and lambs, during spring and summer, based on the digestible protein (DP) content of the diet. (Adapted from Cook et al. 1977.)

Table 2.—Recommended levels of energy and protein for cattle and sheep under range conditions (adapted from Cook and Harris 1968)

Phase of animal metabolism	Digestible energy	Metabolizable energy	Digestible protein
	----- kcal/kg -----		percent
Gestation	1830	1465	4.4
Early lactation and growth	2470	1985	5.4
Late lactation	1940	1545	4.5

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This report is an overview of the biotic and abiotic ecological factors, including the activities of man, that affect forage production on forest and rangeland ecosystems. Also discussed are a review of forage production models, and how forage quantity and quality can control animal production.

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Rocky
Mountains



Southwest



Great
Plains

U.S. Department of Agriculture
Forest Service

Rocky Mountain Forest and Range Experiment Station

The Rocky Mountain Station is one of eight regional experiment stations, plus the Forest Products Laboratory and the Washington Office Staff, that make up the Forest Service research organization.

RESEARCH FOCUS

Research programs at the Rocky Mountain Station are coordinated with area universities and with other institutions. Many studies are conducted on a cooperative basis to accelerate solutions to problems involving range, water, wildlife and fish habitat, human and community development, timber, recreation, protection, and multiresource evaluation.

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*Station Headquarters: 240 W. Prospect St., Fort Collins, CO 80526